

Life habit and spatial distribution of siphonotretid brachiopods in the Lower Ordovician of the Prague Basin, Czech Republic

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ABSTRACT: Siphonotretid brachiopod distribution in the Lower Ordovician of the Prague Basin is described and discussed; the new species *Alichovia cometa* is established. The preservation and distribution of the group indicate a preference for shallow-water offshore, high-energy environments: siphonotretids are abundant shelly fossils in the shallower-water, mostly marginal sites of the basin but are absent in the deeper parts. Their environmental limits were complementary to those of the graptolites; siphonotretids co-occur with epiplanktonic graptolites at only a few localities. Deeper offshore deposits with biramosid dichograptids and diverse, generally delicate benthic dendroids lack siphonotretids. Indeed, siphonotretids were intolerant to dysoxia and preferred a well-aerated siliciclastic, firm sea floor in the shallower parts of the basin. They were tolerant to suspended coarser detritus, using their spines which functioned as an effective sieve. The density and ramification of spines indicate three sifting strategies. Suggested life styles above the seabed on elevated surfaces (algae, sponges, dendroids) are not supported by direct evidence. They more likely lived within more supple and soft matrices (sponges, tufts of algae) stabilised by their spines, with the spinose basket maintaining free space for inhalant and exhalant currents.

KEY WORDS: Brachiopoda, ecology, functional morphology, Graptoloidea, Siphonotretida, spines

Siphonotretid brachiopods have been known for 160 years, since Eichwald (1840) described *Terebratula verrucosa* from the upper Arenig of Ingria (NW Russia). About 20 genera have been described since that time (Holmer & Popov 2000), all characterised by superficial, hollow spines. Siphonotretids rapidly diversified in the Tremadocian and Floian (Bassett *et al.* 1999), although the earliest species of the clade had already appeared in the Middle Cambrian (Aksarina & Pelman 1978). Early Ordovician siphonotretids were preferably distributed across temperate shelves. The early Ordovician siphonotretids are mainly known from Baltica (Sweden, Estonia, SW Russia, Poland and the South Urals), the Perunica Terrane (Czech Republic), and Kazakhstan, but also from Laurentia (Northern Ireland) (reviewed by Bassett *et al.* 1999). The Lower Ordovician peak of siphonotretid diversity was followed by a rapid decline in the Mid Ordovician. The micro-morphic siphonotretids persisted into the Silurian (Mergl 2001a; Valentine *et al.* 2003) with a latest record from the upper Emsian (Mergl 2001b). Despite their attractive morphology, there are only a few reports concerning their distributional patterns and palaeoecology (Biernat & Williams 1971; Wright & Nölvak 1997; Bassett *et al.* 1999).

The main aim of this paper is to analyse the distributional pattern of the siphonotretids in relation to graptolite zonation



and the inferred relative water depth of the Prague Basin; and to discuss the functional morphology of their spines. Siphonotretids achieved a considerable abundance in the Prague Basin, and their diverse morphology may have been correlated with environmental factors and their supposed life modes.

1. Diversity and stratigraphic distribution of Bohemian siphonotretids

In the Ordovician of the Prague Basin, siphonotretids are known from the upper part of the Třenice Formation (Tremadocian), with the latest recorded species in the Králův Dvůr Formation (Katian) (Štorch & Mergl 1989). Before their gradual decline from the Darriwillian onwards, siphonotretids reached a considerable diversity within the Tremadocian and Floian stages (Fig. 1).

Coarse greywackes in lower part of the Třenice Formation (Tremadocian) contain large zhanatellids and obolids (*Hyperobolus* Havlíček, 1982, *Rosobolus* Havlíček, 1982, *Westonisca* Havlíček, 1982, *Libecoviella* Mergl, 1997a) but lack siphonotretids. However, the siphonotretids *Siphonobolus simulans* (Růžička, 1927), *Eosiphonotreta krafti* (Růžička, 1927) and

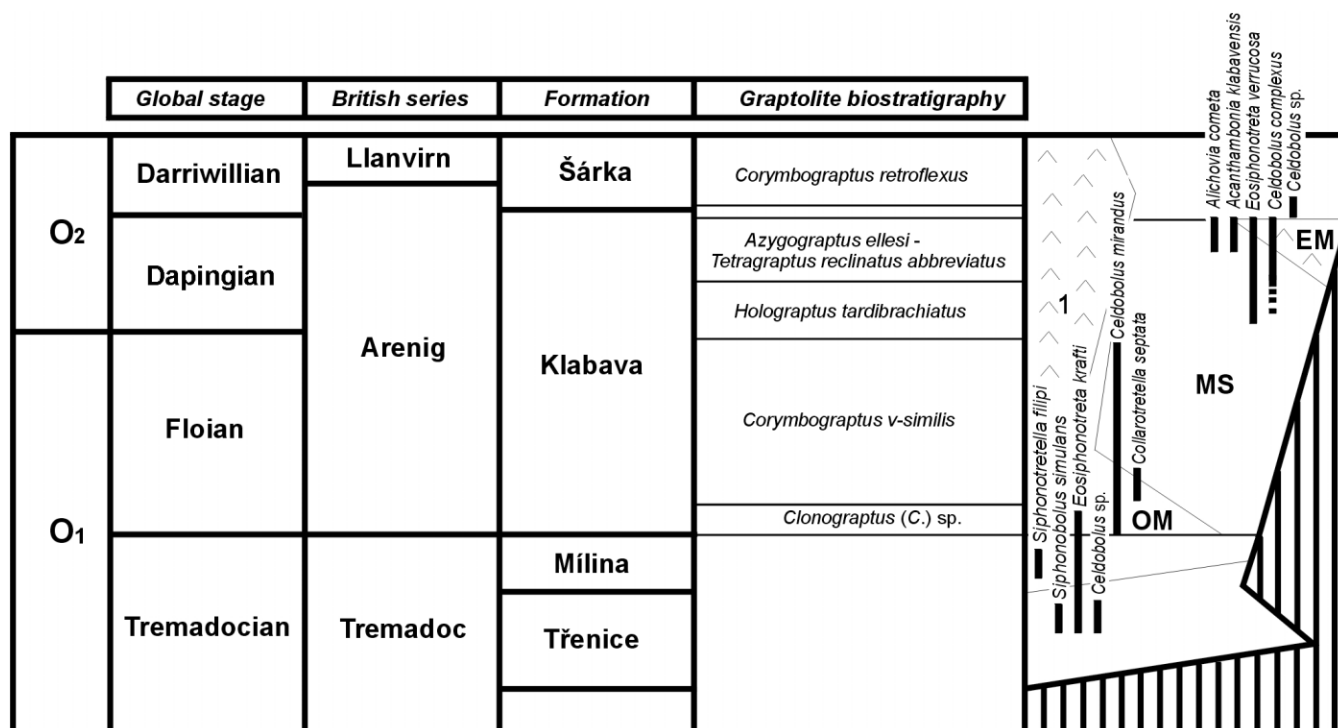


Figure 1 Stratigraphy of the Lower/lower Middle Ordovician in the Prague Basin with the distribution of siphonotretids. Abbreviations: (EM) Ejovice Member; (MS) Mýto Shale; (OM) Olešná Member; (1) volcanites, tuffs and rewashed tuffs. Modified after Kraft & Kraft (2003).

Celdobolus sp. do occur in more offshore associations with medium-sized lingulates, characterised by the presence of *Orbithete* Sdzuy, 1955, *Leptembolon* Mickwitz, 1896 and *Acrotreta* Kutorga, 1848. This association is present in upper part of the Třenice Formation. Siphonotretids in the succeeding Mílina Formation (Upper Tremadocian) are rare, represented only by the micromorphic *Siphonotretella filipi* Mergl, 2002. In both formations, the siphonotretids are a less significant component of lingulate brachiopod associations, and some associations with *Orbithete*, *Leptembolon* and *Acrotreta* lack siphonotretids altogether.

The composition of the lingulate fauna changed with the style of sedimentation in the Klabava Formation. In the red siltstones of the Olešná Member (Floian; Fig. 1), the siphonotretid *Celdobolus* Havlíček, 1982 became dominant; other characteristic taxa are closely related to those of the Mílina Formation, with abundant *Leptembolon*, *Orbithete*, *Elliptoglossa* Cooper, 1956, *Dactyloreta* Rowell & Henderson, 1978, and micromorphic lingulates. The diversity of lingulates was remarkably high, with nearly 20 species. Other siphonotretids, represented by *Siphonotretella filipi*, *Collarotretella septata* Mergl, 1997b, and *Eosiphonotreta* cf. *krafti* are comparatively rare and restricted to few specific horizons. *Celdobolus* occurs throughout all the members of the Klabava Formation. The earlier species, *C. mirandus* (Barrande, 1879) (Olešná Member) is succeeded by *C. complexus* (Barrande, 1879) (Mýto Shale and Ejovice Member). The youngest *Celdobolus* sp. is known from oolitic ferrolites at the base of the Šárka Formation. In general, the morphological variability of all the *Celdobolus* species is conspicuously high, with marked variations in shell size, outline, convexity, wall thickness and density of spinose ornament; recurrent occurrences of these various phenotypes indicate the low taxonomic value of these features. However, development of a pustulose periphery on the shell interior and the shape of pedicle tube both have taxonomic value.

Other siphonotretids are less abundant in the upper Klabava Formation (Dapingian Stage). They are restricted almost exclusively to the higher parts of the Klabava Formation (Mýto Shale and Ejovice Member) with *Acanthambonia klabavensis* Havlíček, 1982, *Eosiphonotreta verrucosa* (Eichwald, 1840) and *Alichovia cometa* sp. nov. locally common.

2. Spatial and vertical distribution of siphonotretids

2.1. Environmental controls on siphonotretids

All the siphonotretids in the Prague Basin are known from fine-grained siliciclastic rocks. Indeed, as suspension feeders, siphonotretids occupied firm substrates consisting of fine sand and silt; instability of muddy substrates prevented their presence in the deeper parts of the basin. Shoreface clastic sediments of the intertidal zone with coarse sand and gravel were also unacceptable as substrates and are thus devoid of siphonotretids. Environmental limits in the basin are consistent with their spatial distribution. Almost all the siphonotretids, and *Celdobolus* above all, are abundant and widespread in the shallow, mostly marginal parts of the basin (Fig. 2). The reports of siphonotretids in the deeper segments of the basin are restricted to sandy sediments near the transgressive base of the Klabava Formation or to heterofacies beds and layers of coarser detritic material, representing slumped material from shallower sites. Grey shales of deep-water origin lack siphonotretids, indicating their intolerance to muddy substrates and dysaerobic water.

2.2. Taphonomy of siphonotretids

In almost all known siphonotretid-bearing sites, the shells of *Celdobolus* are disarticulated and have worn spines. Complete

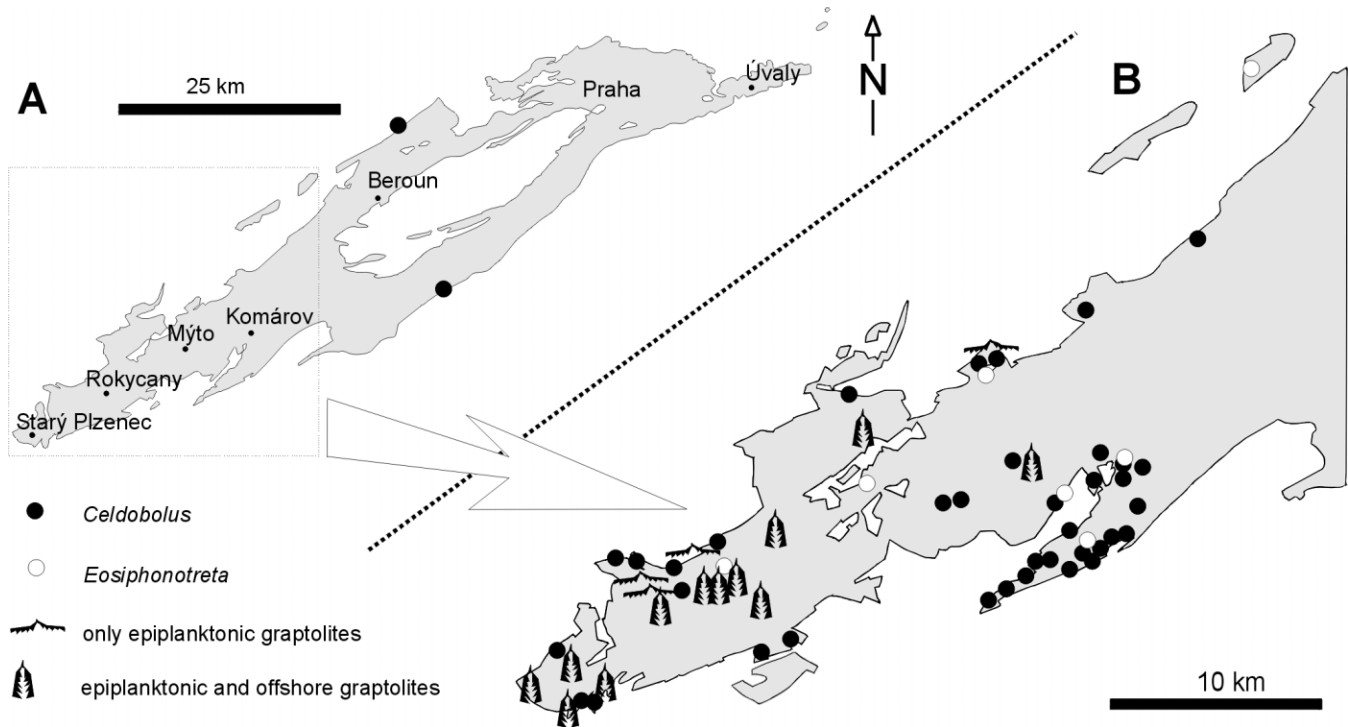


Figure 2 Ordovician of the Prague Basin (A) and detail of its western part (B). Occurrence of *Celdobolus*, *Eosiphonotreta*, and significant epiplanktonic and offshore graptolite fauna localities.

shells with preserved spines are comparatively rare. In general, their valves are disarticulated, broken-off and sometimes associated together in small clusters indicating limited transport (Mergl 1986). However, apart from spine wear, distinct traces of abrasion or bioerosion are unknown. This is consistent with a slightly deeper, offshore environment and minimal oscillatory currents. Angular shell fragments were produced by the episodic release and sorting of collapsed shells from unconsolidated sediment (Mergl 1986). The taphonomy of the shells indicates a low to intermediate sedimentation rate in high energy environments (Brett & Speyer 1990).

In general, the phosphatic shell of siphonotretids is only weakly affected by diagenesis. This is in contrast to the poor preservation or total absence of calcareous (calcitic) shells and organic-walled skeletons (graptolites, chitinozoans), which are not present in the red or dark, brown-violet siltstones and shales and were evidently destroyed by diagenetic processes. Calcareous fossils are preserved only locally and in beds with a higher amount of original calcareous bioclasts. Indeed, in the Lower Ordovician of the Prague Basin, the siphonotretids were a component of moderate diversity communities, with a skeletal biota comprising rhynchonelliform brachiopods, cystoids, sponges, trilobites, rarely also gastropods and other groups.

2.3. Correlation of siphonotretid and graptolite distributions

Occurrences of some siphonotretids can be correlated with the graptolite biozonation and bathymetry of the basin. In a depth-related model of graptolite distribution in the Lower to Middle Ordovician of the Prague Basin, Kraft & Kraft (2002) distinguished a depth stratification of planktonic graptolites during the Floian and Dapingian.

Generally, planktonic graptolites living in open waters above the deeper areas of the Prague Basin have smaller pendent, deflexed or horizontal rhabdosomes (mostly of *Corymbograptus* Obut & Sobolevkaya, 1964, *Didymograptus* M'Coy, 1851). In fossil thanatocoenoses, these dichograptids

are associated with benthic, mostly thin-stiped dendroids with conical to fan-like rhabdosomes with sieve-like framework (*Dictyonema* Hall, 1851, *Desmograptus* Hopkinson in Hopkinson & Lapworth, 1875, *Dendrograptus* Hall, 1858, *Callograptus* Hall, 1865). Brachiopods associated with these thanatocoenoses are rare and restricted to few infaunal or semi-infaunal and thin-shelled obolids (*Paldiskites* Havlíček, 1982) and glossellids (*Rafanoglossa* Havlíček, 1980); siphonotretids are lacking.

Planktonic graptolites living within the epipelagic zone should be present both in shallow and deep offshore and basin-floor deposits. They are represented by large ramose (*Holograptus* Holm, 1881), reclined or declined (*Tetragraptus* Salter, 1863, *Corymbograptus*, *Acrograptus* Tzaj, 1969, *Expansograptus* Bouček & Příbyl, 1951) or unistiped (*Azygograptus* Nicholson & Lapworth in Nicholson, 1875) dichograptids. Benthic dendroids from shallower sea floors have weakly-branched, often arborescent rhabdosomes with free stipes (*Dendrograptus*). Thanatocoenoses with these graptolites are associated with a more diverse and abundant benthic fauna. Brachiopods are represented by acrotretids, dysoristids, acrothelids, and comparatively less dominant infaunal glossellids and thin-shelled obolids. Siphonotretids do occur in this brachiopod association, being represented mostly by small specimens of *Acanthambonia* Cooper, 1956, with rare *Alichovia* Gorjansky, 1969 and *Eosiphonotreta* Havlíček, 1982; *Celdobolus* Havlíček, 1982 is uncommon.

The occurrence of siphonotretids is recurrent in the Klabava Formation. *Celdobolus* is known from some localities with *Corymbograptus v-similis* and *Clonograptus* (C.) biozones (Fig. 3a) and again from the *Azygograptus ellesi*-*Tetragraptus reclinator abbreviatus* Biozone (Fig. 3b), but it is almost unknown from between these two zones. The deep-water associations of the *Corymbograptus v-similis* and *Holograptus tardibrachiatus* biozones have neither *Celdobolus* nor any other siphonotretids. This is consistent with the maximum depth of the basin in the upper *Corymbograptus v-similis* and *Holograptus tardibrachiatus* biozones.

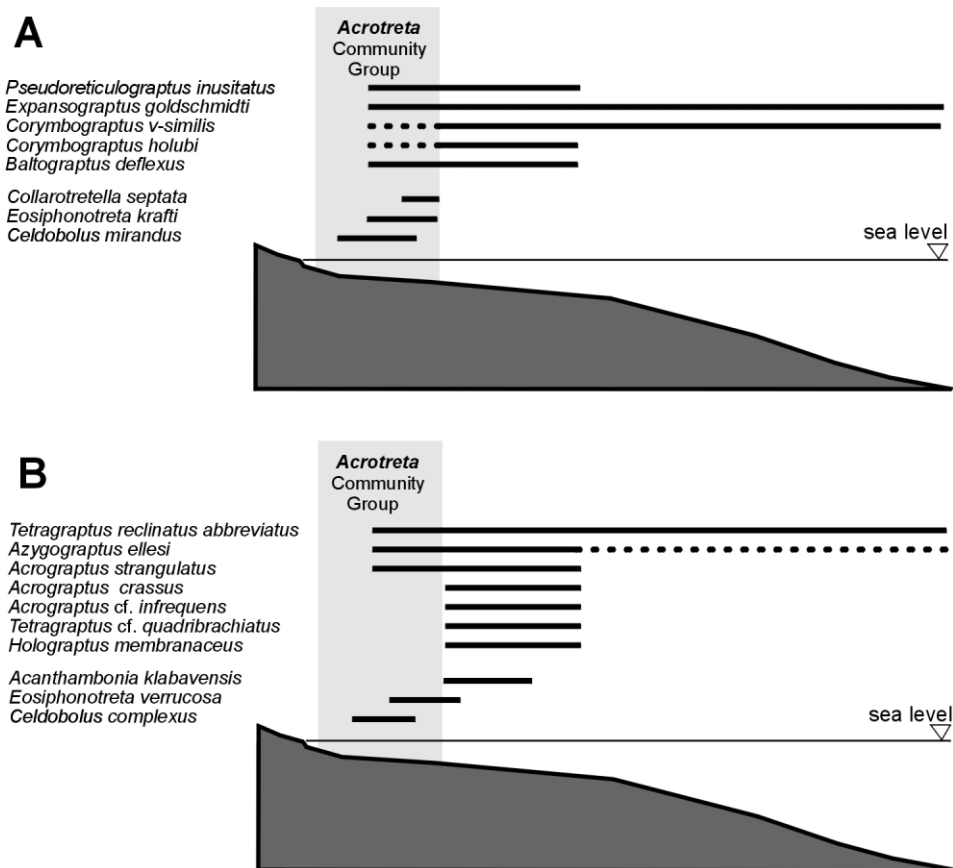


Figure 3 Model of spatial distribution of siphonotretid brachiopod genera and epiplanktonic and offshore, depth-related dichograptids in *Corymbograptus v-similis* Biozone (A) and *Azygograptus ellesi*–*Tetragraptus reclinatus abbreviatus* Biozone (B) along a bathymetric gradient. *Acrotreta* Community Group marked in grey. Modified after Kraft & Kraft (2002) and Mergl (2002).

Celdobolus is conspicuously abundant in the red to brown-violet sediments lacking graptolites (Olešná Member), which are difficult to correlate with more offshore graptolite-bearing successions. Absence of graptolites in these strata is either due to taphonomic or diagenetic controls. Some of these successions with *C. mirandus* are likely to be older or might fall within the *Corymbograptus v-similis* Biozone. Successions with *C. complexus* correlate with the main part of the *Azygograptus ellesi*–*Tetragraptus reclinatus abbreviatus* Biozone.

3. Functional morphology and substrate relationships of siphonotretids

3.1. Pedicle foramen

The shapes of pedicle foramen of siphonotretids (Holmer & Popov 2000) range from a large circular apical opening with a short to long internal tube (*Eosiphonotreta*, *Siphonotreta* De Verneuil, 1845, *Siphonobolus* Havlíček, 1982, *Collarotretella*) an elongate pedicle track posteriorly covered by plate (*Schizambon* Walcott, 1884, *Multispinula* Rowell, 1962) to a minute circular opening without (*Siphonotretella* Popov & Holmer, 1994, *Helmersenina* Pander in von Helmersen, 1861) or with long tube penetrating through the shell wall (*Celdobolus*) or attached to valve floor (*Acanthambonia*). Pedicles of *Schizambon* and *Multispinula* expanded with shell growth and migrated anteriorly leaving a triangular pedicle track. This indicates the importance of the pedicle during the animal's life cycle for stabilisation of an individual on the substrate. Other siphonotretids, well exemplified by *Celdobolus*, had a conspicuously weaker pedicle. The older *C. mirandus* has very narrow

but yet functional pedicle tube while the younger *C. complexus* had an enclosed pedicle tube. Lack of a pedicle tube indicates that shell stability in *Celdobolus* was not achieved by a functional pedicle. Indeed, the taxa with weak or lacking a pedicle tube possessed another strategy to stabilise their shells on the substrate.

3.2. Spines

Hollow tubular spines are the most distinctive feature of the siphonotretids (Biernat & Williams 1971). Their number, shape, and distribution over the shell surface are markedly variable, and these features are characteristic for particular taxa. In general, spines are aligned along growth lamellae, being of uniform size or with two sets of spines; the shape and density are distinctive for particular species. Spines often alternate in successive rows to produce fine meshed array. Arrays of spines near the anterior commissure, formed an interlocking grill during life (Biernat & Williams 1971; Wright & Nölvak 1997). Although spines were remarkably stout in some taxa (*Eosiphonotreta*, *Alichovia*), in other genera (*Gorchakovia* Popov & Khazanovic in Popov *et al.* 1989, *Helmersenina*) the canals perforating the shell did not open into spines but underlay funnel-shaped depressions (antechambers) (Williams *et al.* 2004).

Extensive discussions about spine growth and function of the siphonotretids have been presented by Biernat & Williams (1971), Wright & Nölvak (1997) and (Williams *et al.* 2004). In general, brachiopod spines mostly stabilise the specimen on the sea floor (Rudwick 1965). This is well exemplified by chonetids and productids. A sensory function for the long tubular spines with mantle extensions is unlikely (Williams *et al.* 1997).

Wright & Nölvak (1997) observed, that relationship between the internal diameter of the spines together with the thickening of the spine wall did not alter significantly during growth; both were large. This indicates that the spine walls remained uniformly thick. Assuming organophosphatic shell material in the siphonotretids, the long hollow spines were probably slightly flexible.

Three alternative substrates for siphonotretids have been discussed by Wright & Nölvak (1997). Hook-like spines along the posterior margin of *Acanthambonia* (Wright & Nölvak 1997) suggest the hooking of the growing shells over algal strands or alternatively cylindrical sponge spicules. However, apart from the spines along posterior margin, the other spines are straight and probably did not have an anchorage function. Cementation by the tips of spines to any firm or hard substrate is not possible. It is also unlikely, that brachiopod shells were continually adjacent to or submerged by one valve in sediment, because of the similar distribution of spines on both valves.

Evenly-sized spines oriented subparallel to the commissural plane might have served as a sieve or grill that prevented coarser particles from entering the mantle cavity (Biernat & Williams 1971; Wright & Nölvak 1997; Williams *et al.* 1997). The size of sieve mesh, and thus size of the trapped particles, could be controlled by spine densities along marginal arrays. This function for the spines is also suggested for a number of unrelated brachiopod groups; short spine-like projections with a suggested sieve function surround openings in some athyrids (e.g. *Cleiothyridina* Buckman, 1906) and parazygids (*Parazyga* Hall & Clarke, 1893) (Alvarez & Brunton 2001).

Three types of spinose ornament have been documented amongst the siphonotretids. The first group, with uniformly sized spines, is represented by medium to large-sized *Siphonotreta*, *Siphonobolus* and *Celdobolus*. A uniform size of spines is consistent with their high density over the shell surface of moderate to large shells. The uniform and high density of spines could trap even the smaller particles suspended in water. In *Celdobolus*, the interspaces between the distal parts of spines are approximately 0.1 mm wide and therefore were effective screens for fine sand and larger particles. Thin, uniformly-sized and more widely-spaced spines are present in the micromorphic siphonotretids (*Acanthambonia*, *Siphonotretella*), with similarly-sized spaces in the grills formed by the marginal spines.

The second group comprises siphonotretids with two sets of spines. Larger spines formed an outer grill. More dense arrays of smaller spines form a narrow but dense sieve only along shell periphery. Straining of inhalant currents was in two stages. The outer sieve stopped large particles, the inner sieve fine suspended material. This arrangement was advantageous in environments with the occasional input of large particles, e.g. coarse algal detritus, algal tufts or large volcanic clasts, but only for generally less turbulent water with a low amount of suspended, small particles. This type of spine arrangement is present in the larger siphonotretids (*Eosiphonotreta*). A larger shell size with the flanks held higher above the sea floor was more effective to keep the inhalant currents free of sediment.

The third group had repeatedly-branching spines, with distal and terminal branches crossing each other to constitute a dense screen. The meshes were comparatively small but the total screening area was extensive (Fig. 4). Because the inner sieve is essentially superfluous, the shell surface between bases of large spines is smooth. This type of sieve is known only in *Alichovia*.

4. Substrate of siphonotretids

Whereas the function of spines as a screening basket is highly probable, their function in the stabilisation of shell on the

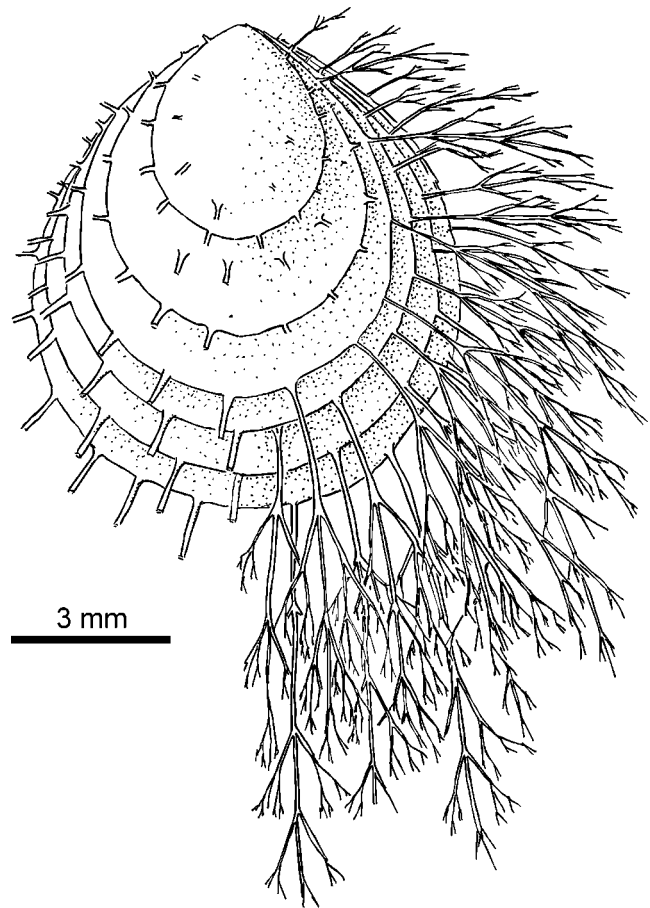


Figure 4 Diagrammatic drawing of dorsal valve of *Alichovia cometa* sp. nov., with partially reconstructed (right) and removed (left) spinose ornament. Scale bar=3 mm.

substrate remains controversial. There are no direct analogies in extant invertebrates. Densely spinose, modern bivalves are not common, and apart from the cementing *Chama* Linnæus, 1758 (Chamidae), only *Spondylus* Linnæus, 1758 (Spondyliidae) possesses long spines on their shell surfaces. Spines of the spondylids are less numerous, mostly stout, although there also are species with numerous delicate spines (e.g. *Spondylus linguefelis* Sowerby, 1847). Spondylids with shell lengths up to 10 cm are far beyond the size limit of siphonotretids. Spines in spondylids did not have a sieve or grill function, and did not form a protective screen. Their spinose surface is often covered by sponges and encrusting invertebrates. Unlike siphonotretids, spondylids are cemented by their right valves to hard surfaces.

Celdobolus possesses remarkably thick-walled, highly convex and subcircular shells. Associated lingulates are either micromorphic (acrotretids, *Rowellella* Wright, 1963) or are larger types, with thin and elongate shells (infaunal habit: *Leptembolon*, *Lingulella* Salter, 1866, *Teneobolus* Mergl, 1995, *Rafanoglossa*) or discoidal shells (epibenthic habit: *Orbithele*). *Celdobolus* was neither infaunal nor quasi-infaunal (Mergl 2002) and its heavy shell is not consistent with a pseudoplanktonic life mode on floating *Sargassum*-like algae.

Spines of uniform size in both valves, posteriorly directed spines, lack of selective abrasion of the early formed spines and the absence of a functional pedicle in some siphonotretids do not favour an epibenthic life mode on mobile silt or sand, neither fixosessile nor reclined nor semi-infaunal. The alternative mode of life for *Celdobolus* and other medium- to small-siphonotretids is above the seabed. Specimens may have been

attached to any elevated substrate: algae, sponges, dendroid graptolites or other hard substrats (e.g., ramose bryozoans).

Sponges. Although a common suggestion (e.g. Bassett *et al.* 1999, Mergl 2002), there is little direct evidence that brachiopods used sponges as a substrate (Gundrum 1979; Conway-Morris & Whittington 1985; Lenz 1993). Mergl (2002) suggested that *Celdobolus* lived above the seabed attached to siliceous sponges, but again there is no direct evidence for this. However, there might be some indirect evidence for another similar substrate; frequently scattered hexactinellid spicules in the Milina Formation are not usually associated with any siphonotretids, with the exception of the micromorphic and rare *Siphonotretella*. On the other hand, shells of *Celdobolus mirandus* in the Olešná Member are often associated with diverse isolated spicules (Mergl & Duršpek 2006) but also with infaunal lingulates indicating the *post-mortem* accumulations of this skeletal detritus. However, shells with preserved spinose ornament are rarely associated with loose spicules and are quite often in siltstones lacking spicules. *Celdobolus complexus* too is rarely associated with spicules, but is common in layers with coarser detritus. Isolated valves of *Eosiphonotreta verrucosa* are often associated with very numerous shells of the micromorphic acrotretid *Numericomma*. Their shells are sometimes very abundant and densely crowded on bedding planes but are never associated with spicules. Therefore it is not likely these brachiopods were attached to sponges. *Siphonobolus simulans* and *Eosiphonotreta krafti* are known from beds with spicules as well as from beds without them; there is no direct relationship in their occurrences.

Nevertheless, a spinose surface is a convenient adaptation for embedding or the slight sinking of a shell below a flexible, compliant or soft matrix, e.g. in algal tufts, demospongian (?) body, in between choanosyncytium and spines of hexactinellid sponges or similar substrates. A juvenile specimen may have fixed the shell by a pedicle to any firm substrate (erect spicule, algal thread). Spines stabilised the shell in the required position as a 'pins' in a surrounding matrix (= 'pincushion'). Fixation by the pedicle would become redundant with the growth of the individual and then the pedicle atrophied, as seen in *Celdobolus complexus*. In addition, the spines protected the specimen from the suffocation of its shell by overgrowth of the surrounding matrix, e.g. growth of a sponge or alga. Spinose cover also maintained enough space between shell and surrounding matrix for the passage of exhalant and inhalant currents.

Dendroids. With erect rhabdosomes, dendroid graptolites are apparently an ideal substrate for the settlement of brachiopod larvae. However, there are no records of attached siphonotretid brachiopods or other shelly fossils. This could be explained by the flexible rhabdosomes that were not rigid enough to maintain heavy, thick-walled shells. In addition, zooids might be able to remove any settled brachiopod larvae.

Hard substrate. Unlike other siphonotretids, *Multispimula* and *Schizambon* possessed an anteriorly-migrating pedicle foramen. In *Mesotreta* Kutorga, 1848 and *Nushbiella* Popov in Kolobova & Popov, 1986 the foramen is nearly subcentral. This is accompanied by a reduction or lack of spinose ornament on shell apices and the development of tangential spines arrays (Cooper 1956; Holmer 1989). Their morphology indicates a life habit with the ventral valve down and attached by a functional pedicle to some sort of firm substrate (e.g. large bioclasts). Arrays of tangential spines in regular concentric bands functioned as a sieve and probably did not support shell stability. This functional morphology is unknown among the siphonotretids in the Prague Basin.

5. Systematic description of *Alichovia*

Genus *Alichovia* Gorjansky, 1969

Type species. *Alichovia ramispinosa* Gorjansky, 1969; Viru Series (Middle Ordovician); Russia.

Alichovia cometa sp. nov.
Figures 4, 5

Holotype. PCZCU 1972; ventral valve figured on Figure 5A, B, deposited in the Palaeontological Collections of the University of West Bohemia, Plzeň, Czech Republic.

Type horizon and locality. Dapingian, Klabava Formation, *Azygograptus ellesi*-*Tetragraptus reclinator abbreviatus* Biozone; Rokycany, highway road section.

Material. Five valves.

Description. Shell biconvex, with moderately thick wall, 8–10 mm long (without spines). Outline subcircular to broadly elliptical, with slightly extended and more rounded anterior than lateral commissure. Commissure rectimarginate. Dorsal valve moderately convex, most convex in posterior one-third of valve length. Ventral valve moderately convex, with apex above low, small subvertical pseudointerarea. Interior of both valves poorly known, with low short median ridge present in dorsal valve.

Postlarval shell covered by 0.5–0.8 mm long concentric growth bands, each of them with steeper sloping anterior border. Surface of each band almost smooth, with weakly-defined growth lines. A row of very long, hollow prostrate spines extending anteriorly, laterally and posterolaterally from steeper anterior slope of each concentric band. Bases of spines evenly arranged, alternating in adjacent bands. Spines remarkably long, rather uniform in shape, ramifying at almost regular distances. Bases of large spines, in anterior sector of large shells, up to 150 µm in diameter, with rather thin wall ca. 30 µm thick. First ramification appears as far as 4–5 mm above the spine base (PCZCU 1972). Deviations of thinner secondary branches occur regularly at 10–20° to axis of the primary spine. Secondary branches lie subparallel to commissural plane. Observed length of secondary spines is 2.2 mm. Lateral branches show subsequent dichotomic (second) or repeated dichotomic (third) bifurcations, extending into very delicate (less than 20 µm in diameter) tubulose spines. Total length of marginal spines comparable with length of shell. The spines on early growth bands rest almost normal to shell surface.

Remarks. *Alichovia* is known from the Tremadocian of Holy Cross Mountains (Biernat 1973) and from Middle Ordovician (Viru Series) of Estonia (Gorjansky 1969); there is a remarkable stratigraphical gap between both occurrences. Our specimens are of Dapingian age. The new species indicates a greater morphological range than that shown by previously-described species, but also shows a stability in the development of its smooth shell surface, devoid of spinose ornament between the bases of large tubulose spines.

The new species differs from the type species *A. ramispinosa* Gorjansky, 1969 by having longer and much more coarsely ramose spines and probably a deeper dorsal valve. All the observed specimens are about half the size of *A. ramispinosa*. *A. analogica* Biernat, 1973 is poorly known, and is characterised by multiramification of spines, which are distantly scattered over the shell surface. *A. analogica* is a very small species, less than 2 mm, and its description is based on immature specimens. Its spines show dichotomic branching (Biernat, 1973; pl. 31, figs 2, 3). The new species is much larger and the

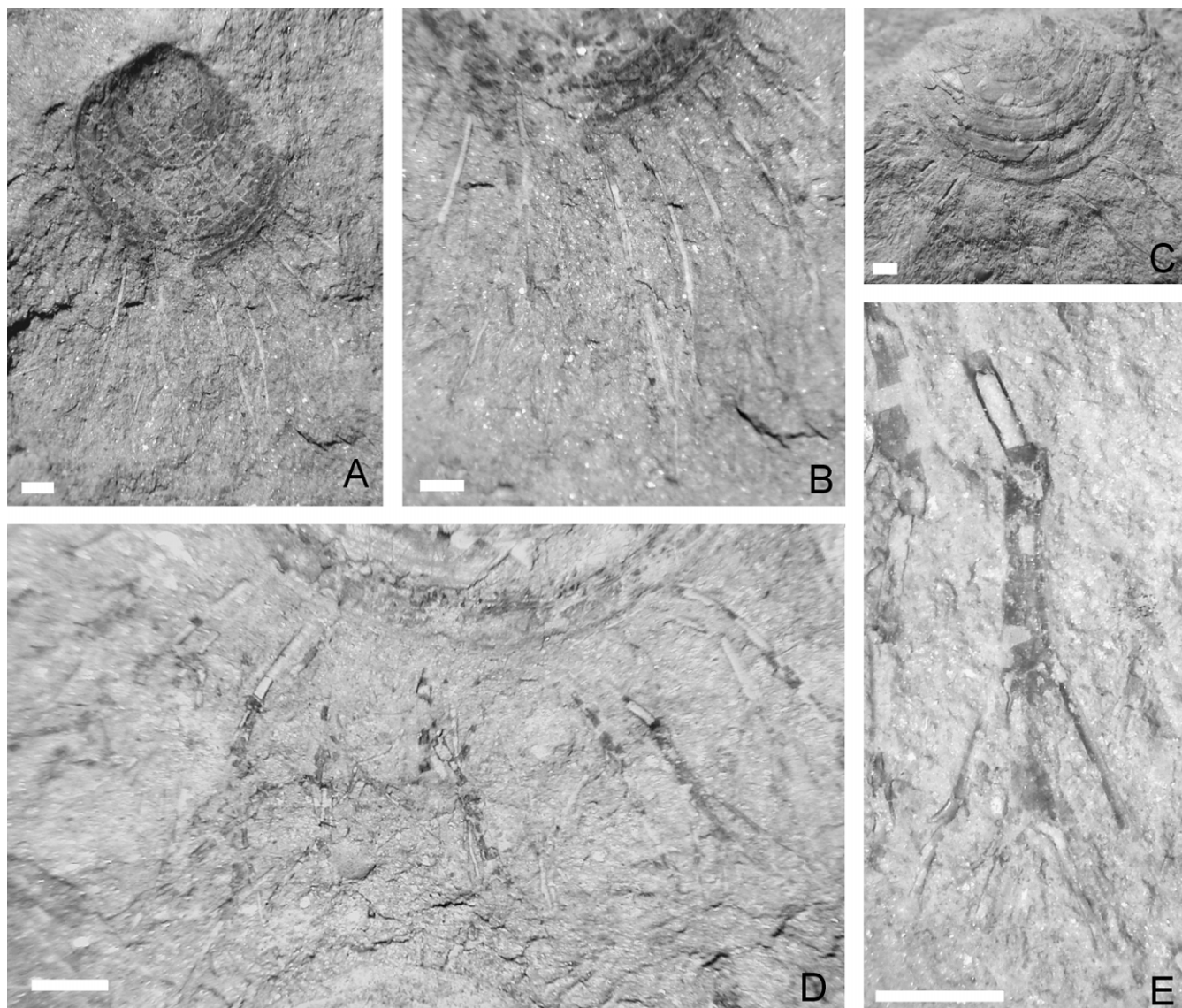


Figure 5 *Alichovia cometa* sp. nov.: (A), (B) Holotype, ventral valve, PCZCU 1972, external mould showing long spines; (C)–(E) Dorsal valve, PCZCU 1973, deformed shell showing: (C) growth lamellae and smooth shell surface; (D) arrays of spines near shell commissure; and (E) ramifying hollow spine with white mineral infillings. All specimens uncovered by ammonium chloride. Scale bars = 1 mm.

spines are laterally ramified with the dichotomic branching restricted to the distal parts of spines.

6. Conclusions

The spatial distribution of siphonotretid brachiopods in the Lower and middle Middle Ordovician of the Prague Basin indicates that this lingulate group preferred shallow marine water with firm substrates and moderately turbulent environments. The prime function of the spines was protection against suspended silt and fine sand entering the mantle cavity. The prominent spines of larger siphonotretids also effectively screened out large particles. Ramified spines screened fine suspended particles by fine distal tips of spines. The rapid decrease in the number of siphonotretids in deeper-water environments, where benthic dendroids ('dendroid gardens') and sunken planktonic dichograptids were often present, was driven by the dominance of excessively fine sediment and poorly oxygenated bottom waters. Siphonotretids were not able to survive the oxygen-deficient waters of black shale deposition during the Darriwillian (Šárka Formation) onwards. Consequently, the decline of the siphonotretids in the

early Mid Ordovician of peri-Gondwana followed the spread of oxygen-depleted bottom waters and the extension of the black-shale lithofacies.

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